Shoot water relations of mature black spruce families displaying a genotype × environment interaction in growth rate. II. Temporal trends and response to varying soil water conditions

JOHN E. MAJOR[1] and KURT H. JOHNSEN[1,2]

[1] Natural Resources Canada, Canadian Forest Service, Atlantic Forestry Centre, Fredericton, NB E3B 5P7, Canada

[2] Current address: USDA Forest Service, Southern Research Station, P.O. Box 12254, 3041 Cornwallis Road, Research Triangle Park, NC 27709, USA

Summary Pressure–volume curves and shoot water potentials were determined for black spruce (*Picea mariana* (Mill.) BSP) trees from four full-sib families at the Petawawa Research Forest, Ontario, Canada. Trees were sampled from a dry site in 1992 and from the dry site and a wet site in 1993. Modulus of elasticity (ε), osmotic potential at turgor loss point (Ψ_{tlp}) and relative water at turgor loss point (RWC_{tlp}) all decreased during the growing season. Osmotic potential at saturation (Ψ_{sat}) and turgor displayed no general temporal trend. Across a range of environmental conditions, Female 59 progeny had equal or lower Ψ_{sat}, and higher or similar ε, mean turgor pressure (P_x) and predawn turgor pressure (P_{pd}) compared with Female 63 progeny. Osmotic potential at saturation decreased as water stress increased from mild to moderate and increased as water stress increased from moderate to severe. Stable genetic differences in Ψ_{sat} were maintained by the same rate of osmotic adjustment from low to moderate water stress. Modulus of elasticity and RWC_{tlp} decreased with decreasing water availability, whereas Ψ_{tlp} showed no response. The combined effects of Ψ_{sat} and ε resulted in no change in P_{pd} as water stress increased from low to moderate values, but turgor declined sharply as water stress increased from moderate to high values. We conclude that drought tolerance traits strongly influence the growth of these black spruce families across sites of varying water availability.

Keywords: genetic variation, osmotic adjustment, turgor, water relations, water stress.

Introduction

From 1991 through 1993, a series of studies were carried out to elucidate the physiological processes contributing to genetic and genotype × environment (G × E) interaction variations observed in a full-sib black spruce experiment planted across sites of varying water availability. Studies have been conducted on shoot growth components (unpublished), gas exchange (Johnsen and Major 1995, Major and Johnsen 1996), and carbon isotope discrimination (Flanagan and Johnsen 1995) of mature black spruce trees. In a companion paper

(Johnsen and Major 1999), we have described site and genetic effects on water relations traits, and shown that turgor-related traits were closely correlated with productivity. In mature trees growing in the field, water relations traits are affected not only by genetic and site factors but also by temporal and environmental factors. In this study, therefore, we examined: (1) temporal variation in water relations traits, (2) responses of water relations traits to soil drying, and (3) the role of osmotic adjustment. Results are interpreted with respect to drought avoidance and drought tolerance mechanisms of the families.

Materials and methods

The four full-sib families of black spruce comprised a two female × two male parent breeding structure and were established with other families as two-year-old stock on three sites in 1973 at the Petawawa Research Forest (Lat. 46° N, Long. 77°30′ W). Full details on genetic sources, plantation location and history, sampling, pressure–volume methodology and estimation of water relations traits are presented in Johnsen and Major (1999).

Correlation analysis was used to test relationships between water relations traits. Predawn xylem water potential (Ψ_{pd}) was used as a measure of soil water potential (Dougherty and Hinckley 1981, Lucier and Hinckley 1982). Previous analyses have indicated that the observed genetic variation is attributable to female parent (Johnsen and Major 1999). Covariate analysis, using female parent, was used to examine water relations trait response to Ψ_{pd}. Effects of female parent were tested by the analysis of covariance of family effects used by Johnsen and Bongarten (1991), with the model $Y_{ij} = B_0 + B_{0i} + B_1 X_{ij} + B_{1i} X_{ij} + E_{ij}$, where Y_{ij} is the dependent variable water relations trait of the jth plant of the ith female parent, B_0 and B_1 are average regression coefficients, B_{0i} and B_{1i} are female parent treatment coefficients, X_{ij} is the independent variable (Ψ_{pd}), and E_{ji} is the error term. In this analysis, three sources of variation are identified: (1) Ψ_{pd} (covariate), (2) female parent and (3) female parent × covariate. Significant female parent effects indicate differences in female parent progeny means (i.e., differences in B_{0i} coefficients, if B_{1i} coef-

ficients are similar) and significant female parent × covariate effects indicate differences in the slopes (B_{1i} coefficients) between female parent progeny. When abrupt changes occurred in linear relationships between variables, inflection points were determined by a simplex algorithm to separate the data for further analysis (Johnsen and Bongarten 1992).

Results

Dry site, 1992

Average maximum, mean and minimum temperatures between July 1 and August 14, 1992 were 22.7, 16.6, and 10.4 °C, and the corresponding temperatures for the six sampling dates were 21.3, 15.7, and 10.0 °C, respectively (Figure 1A). The year's total rainfall was the second highest in the plantation's history (204 mm), with rain occurring over most of the summer (Figure 1B). Decreased Ψ_{pd} values were recorded during the short periods without rain preceding the July 29 and August 11 measurement dates (Figure 1C).

During 1992 on the dry site, osmotic potential at saturation (Ψ_{sat}) decreased during periods of mild drought (Figure 2A). Over all sampling dates, Female 59 progeny had lower or equal Ψ_{sat} compared with Female 63 progeny. Modulus of elasticity (ε) was lowest on July 8 (6.8 MPa) and highest on July 14 (8.3 MPa) and thereafter remained close to the overall mean of 7.9 MPa (Figure 2B). Generally, Female 59 progeny had higher ε than Female 63 progeny.

Osmotic potential at turgor loss point (Ψ_{tlp}) was relatively constant throughout the season (Table 1). Relative water content at turgor loss point (RWC$_{tlp}$) increased from 74.6% to a maximum of 84.1% on July 22, and then decreased later in the season. There were no consistent differences for Ψ_{tlp} and RWC$_{tlp}$ between progeny of the females.

Mean turgor pressure (P_x) increased throughout the measurement period from 0.62 to 0.92 MPa (Figure 2C), and predawn turgor pressure (P_{pd}) followed the same general trend (Table 1). Across all dates, P_{pd} and P_x values were higher or equal for Female 59 progeny compared with Female 63 progeny.
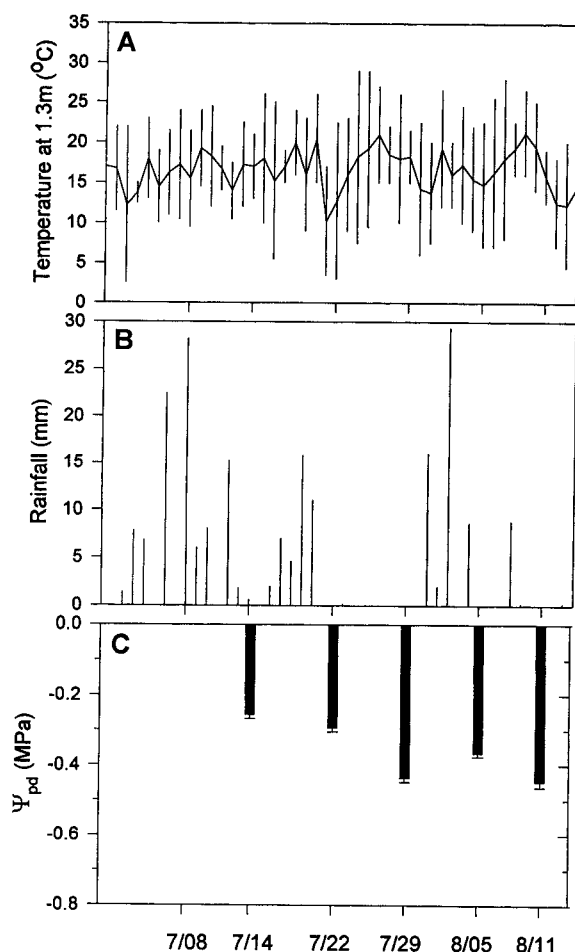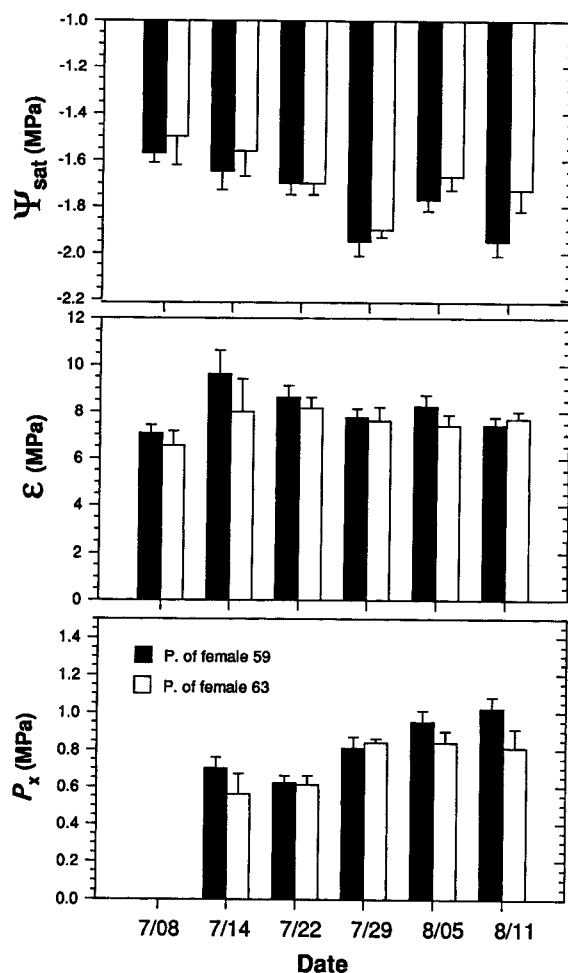

Figure 1. Daily environmental conditions from July 1 to August 14, 1992 at the Petawawa Research Forest, Ontario, Canada, for (A) mean, maximum and minimum temperature, (B) precipitation, and (C) predawn xylem water potential (Ψ_{pd}) (mean and SE) on Site 2 by measurement dates.

Figure 2. Mean and standard error of (A) osmotic potential at saturation (Ψ_{sat}), (B) modulus of elasticity (ε), and (C) mean turgor pressure (P_x) for progeny of Females 59 and 63 on Site 2 in 1992 by measurement dates.

Table1. Mean and standard error of water relations traits by progeny of female for each measurement time in 1992 from Site 2 and for each measurement date in 1993 from Sites 2 and 3. Abbreviations: Ψ_{tlp} = osmotic potential at turgor loss point; RWC$_{tlp}$ = relative water content ar turgor loss point; and P_{pd} = predawn turgor pressure.

Trait	Female	Measurement date						
Site 2 in 1992		July 8	July 14	July 22	July 29	August 5	August 11	
Ψ_{tlp} (MPa)	59	-2.40 ± 0.04	-2.16 ± 0.06	-2.16 ± 0.05	-2.52 ± 0.10	-2.49 ± 0.08	-2.71 ± 0.07	
	63	-2.40 ± 0.12	-2.10 ± 0.12	-2.18 ± 0.08	-2.56 ± 0.05	-2.41 ± 0.06	-2.48 ± 0.12	
RWC$_{tlp}$ (%)	59	75.1 ± 1.00	82.1 ± 1.10	84.1 ± 1.00	81.3 ± 2.00	77.4 ± 1.30	75.3 ± 0.60	
	63	74.1 ± 1.00	81.7 ± 1.80	84.1 ± 1.20	79.8 ± 1.20	77.8 ± 1.40	76.5 ± 1.60	
P_{pd} (MPa)	59	–	1.45 ± 0.09	1.46 ± 0.05	1.62 ± 0.06	1.51 ± 0.05	1.62 ± 0.06	
	63	–	1.36 ± 0.10	1.48 ± 0.05	1.59 ± 0.03	1.40 ± 0.07	1.41 ± 0.09	
Site 2 in 1993		July 5	July 15	July 19	July 23	July 29	August 3	August 9
Ψ_{tlp} (MPa)	59	-2.43 ± 0.12	-2.48 ± 0.06	-2.34 ± 0.13	-2.53 ± 0.08	-2.80 ± 0.12	-2.77 ± 0.12	-2.63 ± 0.12
	63	-2.25 ± 0.06	-2.47 ± 0.15	-2.47 ± 0.10	-2.30 ± 0.08	-2.42 ± 0.10	-2.64 ± 0.06	-2.69 ± 0.20
RWC$_{tlp}$ (%)	59	79.9 ± 3.10	78.9 ± 1.00	78.5 ± 1.30	78.5 ± 1.80	73.0 ± 3.20	75.5 ± 3.10	75.8 ± 3.10
	63	82.6 ± 0.60	80.1 ± 1.60	75.8 ± 2.50	79.8 ± 1.30	73.9 ± 2.60	79.0 ± 2.90	73.8 ± 2.90
P_{pd} (MPa)	59	1.38 ± 0.06	1.46 ± 0.06	1.15 ± 0.08	1.31 ± 0.09	1.80 ± 0.07	1.69 ± 0.07	1.45 ± 0.10
	63	1.35 ± 0.05	1.43 ± 0.09	1.22 ± 0.08	1.02 ± 0.10	1.44 ± 0.09	1.56 ± 0.06	1.30 ± 0.11
Site 3 in 1993		July 5	July 15	July 19	July 23	July 29	August 3	August 9
Ψ_{tlp} (MPa)	59	-2.34 ± 0.10	-2.44 ± 0.11	-2.55 ± 0.07	-2.66 ± 0.13	-2.58 ± 0.05	-2.52 ± 0.10	-2.64 ± 0.08
	63	-2.38 ± 0.13	-2.48 ± 0.04	-2.49 ± 0.05	-2.76 ± 0.08	-2.54 ± 0.11	-2.61 ± 0.04	-2.54 ± 0.11
RWC$_{tlp}$ (%)	59	83.2 ± 2.80	80.3 ± 1.60	79.1 ± 1.50	73.6 ± 1.80	77.0 ± 2.00	81.2 ± 1.30	77.8 ± 2.00
	63	82.7 ± 2.30	78.0 ± 1.70	77.5 ± 0.40	76.2 ± 2.00	78.8 ± 1.30	79.0 ± 3.10	77.0 ± 2.20
P_{pd} (MPa)	59	1.63 ± 0.04	1.59 ± 0.04	1.64 ± 0.09	1.55 ± 0.09	1.81 ± 0.15	1.62 ± 0.06	1.66 ± 0.06
	63	1.57 ± 0.06	1.51 ± 0.06	1.45 ± 0.05	1.57 ± 0.07	1.72 ± 0.13	1.58 ± 0.09	1.44 ± 0.08

Dry site, 1993

The average maximum, mean and minimum temperatures for the 45-day period between July 1 and August 14, 1993, were 26.2, 20.0, and 13.8 °C, and the corresponding temperatures for the seven sampling dates were 27.4, 20.5, and 13.6 °C, respectively (Figure 3A). The 45-day average was 3.4 °C higher in 1993 than in 1992. Annual rainfall in 1993 was about the lowest in the plantation's history (70.1 mm), approximately one third of the 1992 rainfall (Figure 3B). Rainfall preceded measurement days July 29 and August 3 (Figure 3C), resulting in similar Ψ_{pd} values at both sites. On all other measurement days, trees at the dry site had lower Ψ_{pd} than trees at the wet site.

During 1993 on the dry site, mean Ψ_{sat} ranged from -1.75 to -1.90 MPa (Figure 4A). Female 59 progeny generally had lower Ψ_{sat} than Female 63 progeny. Modulus of elasticity progressively increased throughout the season from 4.9 to 7.6 MPa (Figure 4B). Although Female 59 progeny had higher overall ε than Female 63 progeny, rank trends were inconsistent.

Osmotic potential at turgor loss point decreased throughout the measurement period from -2.34 to -2.70 MPa by the last two sampling dates (Table 1). Similarly, RWC$_{tlp}$ decreased from 83 to 74.8% during the season. There were no consistent trends or differences between progeny of females for either trait.

Mean shoot turgor declined to 0.6 MPa on July 19 and 23 (Figure 4C) and then increased to a maximum of 1.10 MPa on August 3 before declining to 0.75 MPa on August 9. Predawn shoot turgor showed a similar pattern with minimum values on July 19 and 23 (1.18 MPa) and maximum values (1.63 MPa) on July 29 and August 3 (Table 1). Generally, Female 59 progeny had higher P_x and P_{pd} than Female 63 progeny.

Wet site, 1993

Osmotic potential at saturation was similar for all measurement dates (Figure 5A). Female 59 progeny had lower or equal Ψ_{sat} values compared with Female 63 progeny for each measurement date. Over the sampling period, ε increased from 4.7 to 8.0 MPa (Figure 5B), and Female 59 progeny had higher ε than Female 63 progeny on all sampling dates.

Osmotic potential at turgor loss point decreased from a maximum of -2.36 MPa on July 5 to a minimum of -2.71 MPa on July 23 and then remained constant (Table 1). Relative water content at turgor loss point fluctuated across dates. There were no consistent trends in female parent rank for RWC$_{tlp}$ or Ψ_{tlp} across dates.

Mean shoot turgor was stable at approximately 0.80 MPa early in the season and then increased to a maximum of 1.18 MPa on July 29 followed by a decrease to 0.86 MPa on the last measurement date (Figure 5C). Predawn shoot turgor was stable across dates (Table 1). Female 59 progeny had higher or equal P_x and P_{pd} compared with Female 63 progeny on all measurement dates.

Environmental responses

When data from 1992 and 1993 was bulked by site and measurement date, Ψ_{sat} decreased as soil water deficit increased
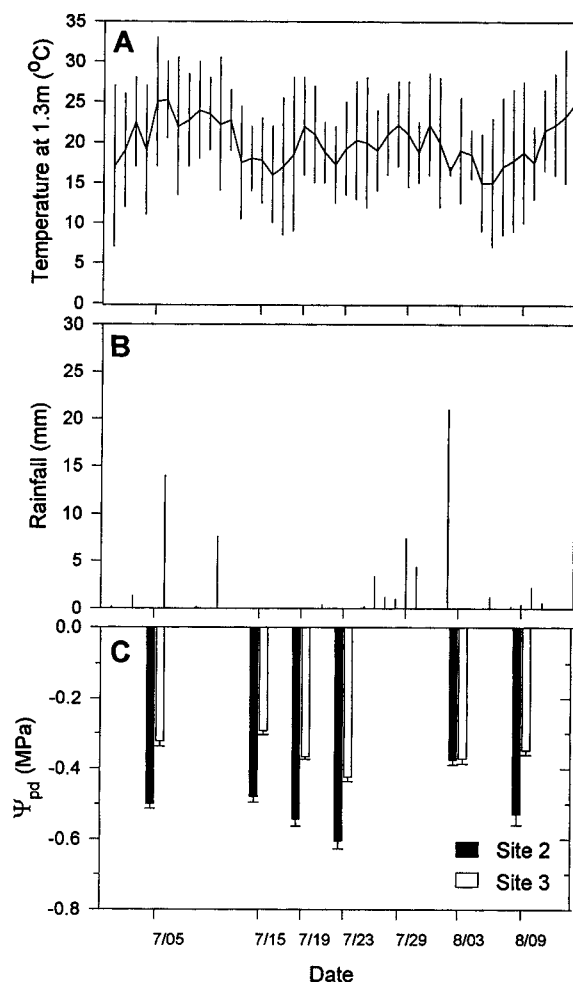
Figure 3. Daily environmental conditions from July 1 to August 14, 1992 at the Petawawa Forest Experiment Station, Ontario, Canada, for (A) mean, maximum and minimum temperature, (B) precipitation, and (C) predawn xylem water potential (Ψ_{pd}) (mean and SE) on Sites 2 and 3 by measurement dates.

Figure 4. Mean and standard error of (A) osmotic potential at saturation (Ψ_{sat}), (B) modulus of elasticity (ε), and (C) mean turgor pressure (P_x) for progeny of Females 59 and 63 on Site 2 in 1993 by measurement dates.

from low to moderate values, but increased as the soil water deficit increased from moderate to high (Figure 6). Based on a simplex algorithm, the inflection point was located at a P_{pd} of −0.41 MPa (Ψ_{sat} = −1.92 MPa). The data on each side of the inflection point were subjected to covariate analysis. On the side of low to medium soil water deficit, covariate analysis indicated that the slopes for the progeny of the females (P = 0.542 for female × Ψ_{pd}) were similar and Female 59 progeny had a lower Ψ_{sat} across Ψ_{pd} than Female 63 progeny (P = 0.011). Overall, covariate analysis showed a significant positive relationship between Ψ_{sat} and Ψ_{pd} (P = 0.004, r = 0.77), with females exhibiting a 0.10 MPa mean difference over the range. On the side of medium to high soil water deficit, covariate analysis indicated no differences in slope between females (P = 0.323 for female × Ψ_{pd}) or female effect (P = 0.679) with a significant relationship between Ψ_{sat} and Ψ_{pd} (P < 0.001, r = 0.84) over the range.

Modulus of elasticity decreased as soil water deficit increased (P = 0.021, r = 0.40) (Figure 7A). Covariate analysis
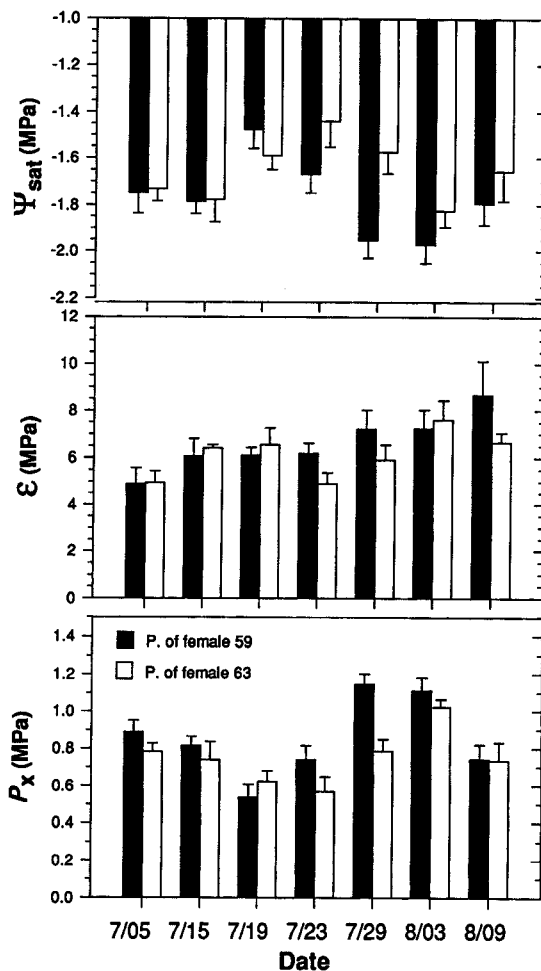
indicated no differences in slope between progeny of the females (P = 0.510 for female × Ψ_{pd}) or female effect (P = 0.101). Modulus of elasticity ranged from 7.80 MPa at low soil water deficit (Ψ_{pd} = −0.25 MPa) to 5.67 MPa at high soil water deficit is (Ψ_{pd} = −0.65 MPa). Relative water content at turgor loss point decreased as soil water deficit increased (P = 0.018, r = 0.40) (Figure 7B), whereas Ψ_{tlp} showed no significant relationship (P = 0.117, r = 0.27). Analysis of covariance for RWC$_{tlp}$ indicated no differences in slope between progeny of the females (P = 0.549 for female × Ψ_{pd}) or female effect (P = 0.934). Mean RWC$_{tlp}$ was 80.7 and 76.2% at low and high soil water deficits, respectively.

The response of P_{pd} to Ψ_{pd} displayed a distinct inflection point (Ψ_{pd} = 0.408 MPa) similar to the response of Ψ_{sat} (Ψ_{pd} = 0.410 MPa) (Figure 8). From mild to moderate soil water deficit, P_{pd} showed no significant linear relationship to Ψ_{pd} (P = 0.101, r = 0.40), although the female effect was statistically significant with P_{pd} values of 1.58 and 1.48 MPa for progeny of Females 59 and 63, respectively (P = 0.017, r =
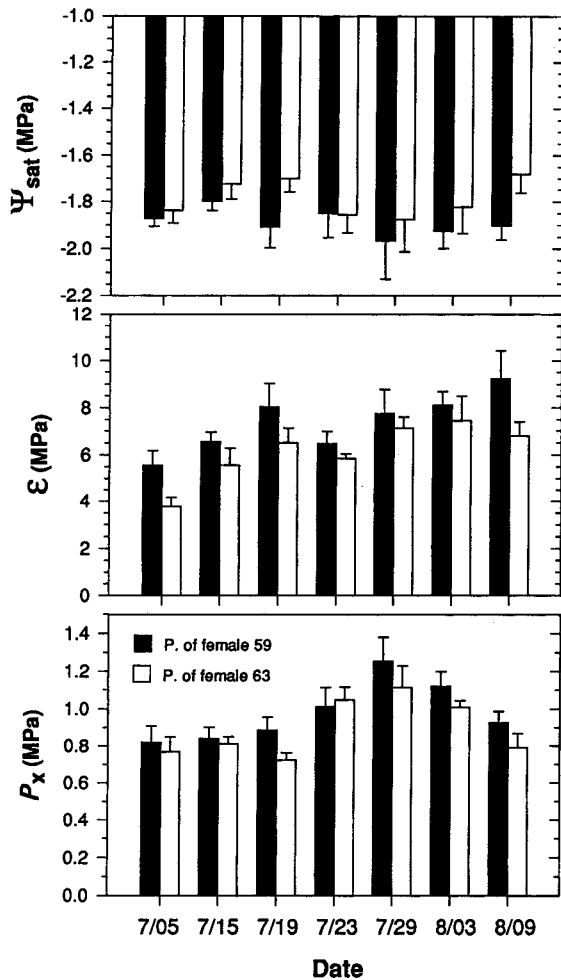
Figure 6. Relationships between osmotic potential at saturation (Ψ_{sat}) (mean ± SE) and predawn xylem water potential (Ψ_{pd}) (mean ± SE) for progeny of Females 59 and 63. Equations from analysis of covariance from low water stress to inflection point: progeny of Female 59, $y = -1.339 + 1.48x$; progeny of Female 63, $y = -1.232 + 1.484x$: $r = 0.77$ ($P = 0.004$). Equation from analysis of covariance from inflection point to high water stress: $y = 2.716 - 1.961x$: $r = 0.84$ ($P < 0.001$).

Figure 5. Mean and standard error of (A) osmotic potential at saturation (Ψ_{sat}), (B) modulus of elasticity (ε), and (C) mean turgor pressure (P_x) for progeny of Females 59 and 63 on Site 3 in 1993 by measurement dates.

0.53). From moderate to high soil water deficits, P_{pd} decreased from a high of approximately 1.58 MPa at the inflection point to 1.03 MPa at high soil water deficits ($P < 0.001$, $r = 0.90$). Covariate analysis indicated no differences in slope between progeny of the females ($P = 0.348$ for female × Ψ_{pd}) or female progeny effect ($P = 0.633$). Mean shoot turgor pressure showed no significant relationship to soil water deficit ($P = 0.368$, $r = 0.16$) and no female effect ($P = 0.184$).

Discussion

Temporal and spatial variation

A plant's ability to tolerate drought changes during the year. Typically, plants are most drought tolerant during the winter and least drought tolerant during spring bud flush (Ritchie and Shula 1984, Colombo 1987, Grossnickle 1989, Grossnickle and Russell 1996). Furthermore, water relations traits change in response to phenology, temperature, daylength and water
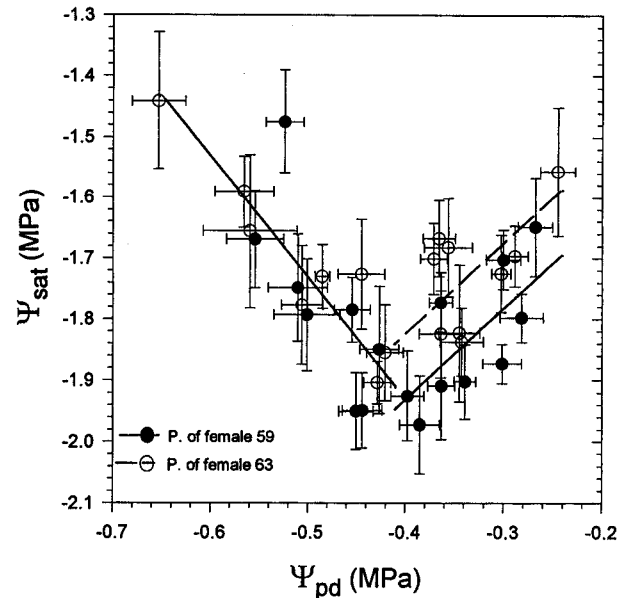
availability. We assessed temporal trends in water relations traits at a dry site in a wet year (1992), a wet site in a dry year (1993) and a dry site in a dry year (1993).

Osmotic potential at saturation was more sensitive to changes in soil water content than measurement date. In the wet year (1992), Ψ_{sat} decreased only slightly over the season, whereas there was no temporal trend in Ψ_{sat} at either site in the dry year (1993). Values were similar for both sites except during a very dry period between July 15 and 29 when Ψ_{sat} was significantly higher in trees on the dry site than in trees on the wet site. That is, Ψ_{sat} increased rather than decreased as might be expected if there had been continued osmotic adjustment during the driest period.

Values of Ψ_{tlp} were similar for trees at both sites as a result of compensatory effects of lower Ψ_{sat} and higher ε on the wet site versus higher Ψ_{sat} and lower ε on the dry site. Compensatory changes have been observed for well-watered and water-stressed seedlings (Kwon and Pallardy 1989, Grossnickle and Russell 1996) and for plants subjected to other stress treatments (Nabil and Coudret 1995, Momen and Helms 1996).

Although ε did not vary significantly with site (Johnsen and Major 1999), it was greater on the wet than on the dry site on most measurement dates. These data are consistent with expectations that, under dry conditions, the elasticity of shoot tissue is adjusted to maintain turgor (Parker and Pallardy 1988, Tschaplinski and Blake 1989).

The highest and lowest turgor values were associated with the highest and lowest Ψ_{pd} values. Generally, predawn shoot turgor was higher in trees on the wet site than in trees on the
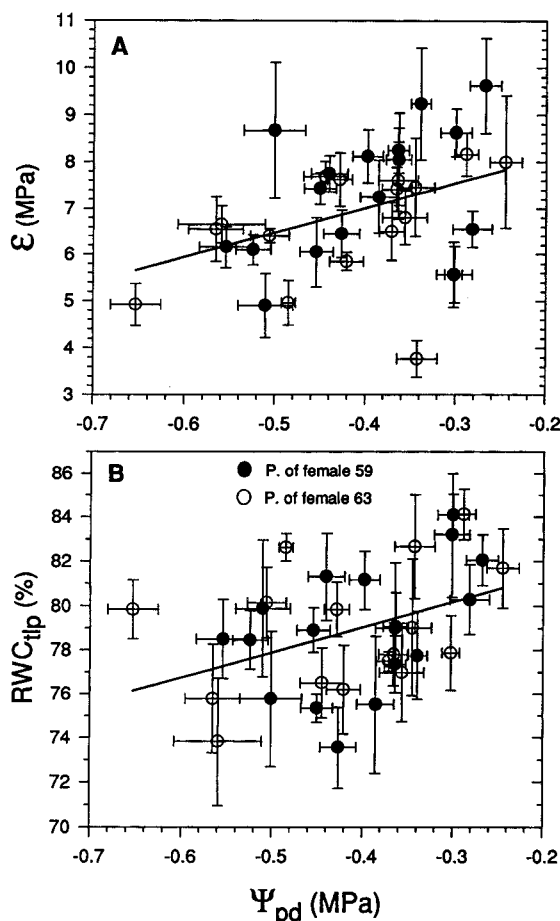
Figure 7. Relationships between (A) modulus of elasticity (ε) (mean ± SE) and (B) relative water content at turgor loss point (RWC$_{tlp}$) (mean ± SE) and predawn xylem water potential (Ψ_{pd}) (mean ± SE) for progeny of Females 59 and 63. Equation from analysis of covariance for modulus of elasticity: $y = 9.14 + 5.34x$: $r = 0.40$ ($P = 0.021$) and for relative water content at turgor loss point: $y = 83.6 + 11.4x$: $r = 0.40$ ($P = 0.018$).

Figure 8. Relationships between predawn turgor (P_{pd}) (mean ± SE) and predawn xylem water potential (Ψ_{pd}) (mean ± SE) progeny for Females 59 and 63. Equations from analysis of covariance from low water stress to inflection point: progeny of Female 59, $y = 1.583$; progeny of Female 63, $y = 1.48$: $r = 0.53$ ($P = 0.023$). Equation from analysis of covariance from inflection point to high water stress: $y = 2.58 + 2.37x$: $r = 0.90$ ($P < 0.001$).

dry site. Mean shoot turgor did not display a strong correlation with soil water availability, because the relationship was masked by vapor pressure deficit effects (Hinckley et al. 1978).

Response of water relations traits to varying soil water content

The Ψ_{pd} data, obtained from ≥ 20-year-old trees with extensive root systems demonstrated a high sensitivity to soil drying. Other studies with black spruce trees conducted under natural soil drying conditions have shown that most gas exchange and water relations effects occur at Ψ_{pd} values above −1.0 MPa, (Grossnickle 1993, Grossnickle and Major 1994, Stewart et al. 1995).

We expected that Ψ_{sat} would decrease with decreasing soil water availability in agreement with the conventional concept of active osmotic adjustment. We found stable genetic differences in Ψ_{sat}, maintained by the same rate of osmotic adjustment from low to moderate stress. Using seedlings of the same
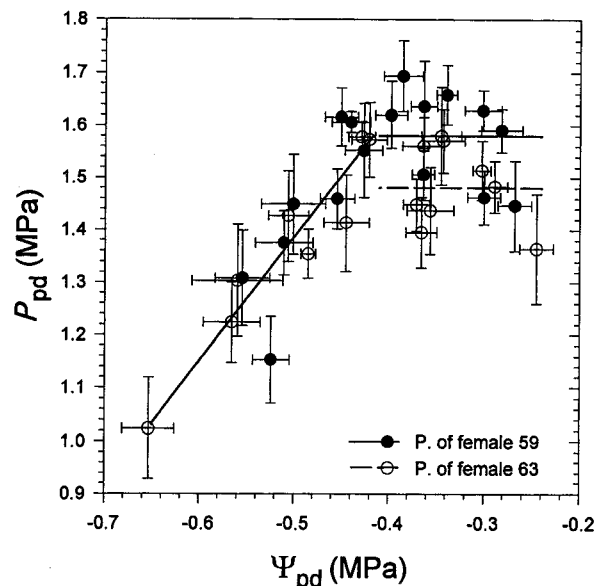
families in a growth chamber experiment, Tan et al. (1992b) concluded that there was little genetic variation in osmotic potential measured in unstressed seedlings, and that Female 59 progeny had greater osmotic adjustment with increasing PEG-induced water stress. The discrepancies between Tan et al. (1992a, 1992b) and our water relations study results are considerable, and the physiological mechanisms advanced are quite different. First, to accurately examine active osmotic adjustment, one should assess Ψ_{sat} under different degrees of stress and not compare osmotic potential at different xylem water potentials (Ψ_x) (Tan et al. 1992b, Fig 1B), as osmotic potential is confounded by passive adjustment (Tyree and Jarvis 1982, Tesky and Hinckley 1986). Second, the discord may also be attributable to the use by Tan et al. (1992a, 1992b) of PEG to induce water stress. The effect of PEG on plant physiological responses may have lead to a direct and differential effect (Lawlor 1970, Chazen et al. 1995, Fan and Blake 1997). Also, they induced a "brief" set of three, three-day treatments. Rate and frequency at which drought is imposed in greenhouse, and laboratory experiments can often influence water relations traits (Abrams 1988, Grossnickle and Russell 1996).

Following initial osmotic adjustment to moderate water stress, Ψ_{sat} increased with increasing water stress (cf. Kwon and Pallardy 1989). The increase in Ψ_{sat} may be the result of net loss of solutes. Electrolyte leakage through the cell membrane often occurs in response to drought (Kuhns et al. 1993, Gebre et al. 1994). In a study of seedlings of the same families, Tan and Blake (1993) reported that electrolyte leakage in

Female 63 progeny was twice that in Female 59 progeny (25 versus 12.8%), at a daytime Ψ_x of -2.0 MPa. In our study, the response of Ψ_{sat} to decreases in Ψ_{pd} beyond the inflection point of -0.4 MPa did not differ between the progeny of the two females, suggesting that the progeny did not differ in electrolyte leakage. Another possible contribution to the increase in Ψ_{sat} at high soil water deficits may result from a reduction in the accumulation of cellular carbohydrates in response to a decrease in net photosynthesis (Koppenaal et al. 1991).

Increasing elasticity of cell walls during drought can provide an important contribution to drought tolerance (Colombo 1987, Kozlowski et al. 1991) because it allows turgor to be maintained as water is lost. Although cell wall elasticity explained less than 20% of the variation, it did increase with soil water deficit. Covariate analysis showed no differences between progeny of the females—although we observed a contrast based on ANOVA (Johnsen and Major 1999)—indicating that ε had no, or even a negative contribution to drought resistance. Relative water content at turgor loss point decreased slightly with increasing soil water deficit, probably as a result of simultaneous adjustments in elasticity.

A primary effect of reduced water availability is decreased cell turgor, which decreases cell enlargement and growth (Hsiao and Jing 1987). Although P_{pd} was constant as soil water deficits increased from low to moderate values, further increases in soil water deficit resulted in a large reduction in P_{pd}. The maintenance of P_{pd} at moderate soil deficits was largely a result of active osmotic adjustment. However, beyond the inflection point, P_{pd} decreased sharply because of both increased osmotic potential and decreased water availability.

Importance of drought avoidance and drought tolerance mechanisms

Plant water relations traits, and the way they contribute to overall drought resistance, vary with plant species, families and, perhaps, populations within species. Selection for drought avoidance is a resonable strategy for deployment on very dry sites where survival is of utmost concern. Traits such as Ψ_{tlp}, RWC_{tlp}, and cuticular transpiration can contribute directly to water conservation and constitute drought avoidance traits. However, in our study, Ψ_{tlp}, RWC_{tlp}, and cuticular transpiration (unpublished data) displayed no consistent trends between progeny of females or between sites. Furthermore, Ψ_{tlp} and RWC_{tlp} were poorly related to productivity (Johnsen and Major 1999), and stomatal control showed no consistent trends between progeny of females or between sites (Major and Johnsen 1996). Thus, we conclude that drought avoidance mechanisms are not important with respect to drought resistance of these families on these sites.

Drought tolerance traits such as ε, Ψ_{sat} and turgor allow growth to continue during periods of moderate drought (White et al. 1996). For example, high cell wall elasticity results in enhanced drought tolerance because higher elasticity can maintain higher turgor for a given relative water content. In our study, Female 59 progeny had lower cell wall elasticity than Female 63 progeny; however, because genetic differences in Ψ_{sat} outweighed genetic differences in cell wall elasticity,

shoot turgor was higher in Female 59 progeny than in Female 63 progeny. There was also a strong G × E trend in P_{pd} and mean family P_{pd} was strongly related to growth across all sites (Johnsen and Major 1999). In addition, genetic variation in net photosynthesis was consistent over a range of soil water conditions and displayed a differential response to vapor pressure deficit that was largely non-stomatal (Major and Johnsen 1996). We conclude that drought tolerance traits such as Ψ_{sat}, ε, turgor and net photosynthetic responses to water stress have large effects on the growth rate and stability of these families across sites of varying water availability.

References

Abrams, M.D. 1988. Sources of variation in osmotic potentials with special reference to North American tree species. For. Sci. 34:1030–1046.

Chazen, O., W. Hartung and P.M. Neumann. 1995. The different effects of PEG 6000 and NaCl on leaf development are associated with differential inhibition of root water transport. Plant Cell Environ. 18(7):727–735.

Colombo, S.J. 1987. Changes in osmotic potential, cell elasticity, and turgor relationships of 2nd-year black spruce container seedlings. Can. J. For. Res. 17:365–369.

Dougherty, P.M. and T.M. Hinckley. 1981. The influence of a severe drought on net photosynthesis of white oak (*Quercus alba*). Can. J. Bot. 59:335–341.

Fan, S. and T.J. Blake. 1997. Comparison of polyethlene glycol 3350 induced osmotic stress and soil drying for drought simulation in three woody species. Trees 11:342–348.

Flanagan, L.B. and K.H. Johnsen. 1995. Genetic variation in carbon isotope discrimination and its relationship to growth under field conditions in full-sib families of *Picea mariana*. Can. J. For. Res. 25:39–47.

Gebre, G.M., M.R. Kuhns and J.R. Brandle. 1994. Organic solute accumulation and dehydration tolerance in three water-stressed *Populus deltoides* clones. Tree Physiol. 14:575–587.

Grossnickle, S.C. 1989. Shoot phenology and water relations of *Picea glauca*. Can. J. For. Res. 19:1287–1290.

Grossnickle, S.C. 1993. Shoot water relations and gas exchange of western hemlock and western red cedar seedlings during establishment on a reforestation site. Trees 7:148–155.

Grossnickle, S.C. and J.E. Major. 1994. Interior spruce seedlings compared with emblings produced from somatic embryogenesis: II. Stock quality assessment prior to field planting. Can. J. For. 24:1385–1396.

Grossnickle, S.C. and J.H. Russell. 1996. Changes in shoot water relations parameters of yellow-cedar (*Chamaecyparis nootkatensis*) in response to environmental conditions. Can. J. Bot. 74:31–39.

Hinckley, T.M., J.P. Lassoie and S.W. Running. 1978. Temporal and spatial variations in water status of forest trees. For. Sci. Monogr., Bethesda, MD, 72 p.

Hsiao, T.C. and J. Jing. 1987. Leaf and root expansive growth in response to water deficits. *In* Physiology of Cell Expansion During Plant Growth. Eds. D.J. Cosgrove and D.P. Knievel. The American Society of Plant Physiologists, Rockville, MD, pp 180–192.

Johnsen, K.H. and B.C. Bongarten. 1991. Allometry of acetylene reduction and nodule growth of *Robinia pseudoacacia* families subjected to varied root nitrate concentrations. Tree Physiol. 9:507–522.

Johnsen, K.H. and B.C. Bongarten. 1992. Relationships between nitrogen fixation and growth in *Robinia pseudoacacia* seedlings: A functional growth-analysis approach using [15]N. Physiol. Plant. 86:77–84.

Johnsen, K.H. and J.E. Major. 1995. Gas exchange of 20-year-old black spruce families displaying a genetic × environmental interaction in growth rate. Can. J. For. Res. 25:430–439.

Johnsen, K.H. and J.E. Major. 1999. Shoot water relations of mature black spruce families displaying a genotype × environment interaction in growth rate. I. Family and site effects over three growing seasons. Tree Physiol. 19:367–374.

Koppenaal, R.S., T.J. Tschaplinski and S.J. Colombo. 1991. Carbohydrate accumulation and turgor maintenance in seedling shoots and roots of two boreal conifers subjected to water stress. Can. J. Bot. 69:2522–2528.

Kozlowski, T.T., P.J. Kramer and S.G. Pallardy. 1991. The physiological ecology of woody plants. Academic Press Inc., San Diego, CA, 657 p.

Kuhns, M.R., W.W. Stroup and G.M. Gebre. 1993. Dehydration tolerance of five bur oak (*Quercus macrocarpa*) seed sources from Texas, Nebraska, Minnesota, and New York. Can. J. For. Res. 23:387–393.

Kwon, K.W. and S.G. Pallardy. 1989. Temporal changes in tissue water relations of seedlings of *Quercus acutissima, Q. alba, and Q. stellata* subjected to chronic water stress. Can. J. For. Res. 19:622–626.

Lawlor, D.W. 1970. Absorption of polyethylene glycols by plants and their effects on plant growth. New Phytol. 69:501–513.

Lucier, A.A. and T.M. Hinckley. 1982. Phenology, growth and water relations of irrigated and non-irrigated black walnut. For. Ecol. Manag. 4:127–142.

Major, J.E. and K.H. Johnsen. 1996. Family variation in photosynthesis of 22-year-old black spruce: a test of two models of physiological response to water stress. Can. J. For. Res. 26:1922–1933.

Momen, B. and J.A. Helms. 1996. Osmotic adjustment induced by elevated ozone: interactive effects of acid rain and ozone on water relations of field-grown seedlings and mature trees of *Pinus ponderosa*. Tree Physiol. 15:799–805.

Nabil, M. and A. Coudret. 1995. Effects of sodium chloride on growth, tissue elasticity and solute adjustment in two *Acacia nilotica* subspecies. Physiol. Plant. 93:217–224.

Parker, W.C. and S.G. Pallardy. 1988. Pressure–volume analysis of leaves of *Robinia pseudoacacia* L. with the sap expression and free transpiration methods. Can. J. For. Res. 18:1211–1213.

Ritchie, G.A. and R.G. Shula. 1984. Seasonal changes of tissue-water relations in shoots and root systems of Douglas-fir seedlings. For. Sci. 30:538–548.

Stewart, J.D., A. Zine El Abidine and P.Y. Bernier. 1995. Stomatal and mesophyll limitations of photosynthesis in black spruce seedlings during multiple cycles of drought. Tree Physiol. 15:57–64.

Tan, W. and T.J. Blake. 1993. Drought tolerance, abscisic acid and electrolyte leakage in fast- and slow-growing black spruce (*Picea mariana*) progenies. Physiol. Plant. 89:817–823.

Tan, W., T.J. Blake and T.J.B. Boyle. 1992*a*. Drought tolerance in faster- and slower-growing black spruce (*Picea mariana*) progenies: I. Stomatal and gas exchange responses to osmotic stress. Physiol. Plant. 85:639–644.

Tan, W., T.J. Blake and T.J.B. Boyle. 1992*b*. Drought tolerance in faster- and slower-growing black spruce (*Picea mariana*) progenies: II. Osmotic adjustment and changes of soluble carbohydrates and amino acids under osmotic stress. Physiol. Plant. 85:645–651.

Teskey, R.O. and T.M. Hinckley. 1986. Moisture: effects of water stress on trees. *In* Stress Physiology and Forest Productivity. Eds. T.C. Hennessey, P.M. Dougherty, S.V. Kossuth and J.D. Johnson. Kluwer Academic Publishers, Hingham, MA, pp. 9-33.

Tschaplinski, T.J. and T.J. Blake. 1989. Water-stress tolerance and late season organic solute accumulation in hybrid poplar. Can. J. Bot. 67:1681–1688.

Tyree, M.T. and P.G. Jarvis. 1982. Water in tissues and cells. *In* Encyclopedia of Plant Physiol. Vol. 12B. Eds. O.L. Lange and J.D. Bewley. Springer-Verlag, Berlin, pp. 36-77.

White, D.A., C.L. Beadle and D. Worledge. 1996. Leaf water relations of *Eucalyptus globulus* ssp. *globulus* and *nitens: seasonal, drought and species effects. Tree Physiol. 16:469–476.*